PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Researches on the Structure, Organization, and Classification of the Fossil Reptilia. Part IX., Section 2. The Reputed Mammals from the Karroo Formation of Cape Colony

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XXII. *Researches on the Structure, Organization, and Classification of the Fossil Reptilia.*—Part IX., Section 2. *The reputed Mammals from the Karroo formation of Cape Colony.*

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[Plate 89.]

The reputed Mammals from the Karroo.

1. *On Theriodesmus phylarchus.*

In 1887, I described some associated bones of an animal from Klipfontein, Fraserberg, under the name *Theriodesmus phylarchus* ('Phil. Trans.,' 1888, B., 24). The fossil has since received some attention from anatomists, but I am not aware that the place originally assigned to it among the mammalia has been questioned. Professor Carl Bardeleben ('Proc. Zool. Soc.,' 1889, p. 259), who critically examined some points of my interpretation, concurred that it cannot be said to belong to any known order of mammals; and affirms that it is not a reptile in the modern sense of the word. He states that its characters are such that it might be placed between reptiles and mammals, but does not offer evidence or argument in support of that determination. This is not a substantial difference from my own conclusion, which regarded *Theriodesmus* as illustrating the reptilian inheritance in the mammalian hand. These conclusions may be re-examined in the light of new evidence which I obtained in South Africa. Before stating that evidence I propose to examine the interpretation of the carpus and phalanges which Professor Bardeleben offers in place of that given in my paper, published in the 'Philosophical Transactions.'

Professor Bardeleben places four bones in the proximal row of the carpus instead of the three bones shown in my restoration. The result of this is to make the carpus wider than the distal ends of the ulna and radius, so that in his restoration the radius only covers a small portion of the smooth proximal articular surface of the bone named by me scapho-lunar, and by him named scaphoid. That proximal surface shows no evidence of division into two parts, and, therefore, the hypothetical position assigned to it is not supported by evidence. The proposal to name the bone scaphoid is based upon the hypothesis that I have mistaken the lunar bone for the central bone; and the discovery of this supposed error is the ground for introducing four bones into the

proximal row of the carpus. No argument is offered in support of that interpretation, and no South African fossil is known with the undisturbed carpus composed in that way. In the fossil the carpus is manifestly somewhat displaced, though there is no question that the three bones which I have regarded as proximal are substantially in their natural positions; and that the bones of the distal row of the carpus are also in their natural positions, in contact with the metacarpal bones. The transverse width over these four distal bones is one-tenth of an inch less than the transverse width over the three bones which I placed in the proximal row. The difference of interpretation is therefore with the bones which I regarded as central bones. These bones are entirely distal in position to the proximal carpal bone, which is in contact with the distal end of the radius; so that, as preserved, the bone which seems to me to be the principal central bone is between the magnum and the outer side of the bone which articulates with the radius; and that central bone which Professor BARDELEBEN identifies as the lunar bone, is in close lateral contact on its inner side with the bones which he regards as central. There is, I submit, no evidence for the suggested transposition of the bone from the middle row of the carpus to the proximal row; and no argument is offered in support of the change of interpretation. The distal end of the radius gives no indication of having supported two bones; while on the outer distal surface of the scapho-lunar is a distinct facet which seems to correspond in size and position with the central bone which is below it.

It is, I think, unnecessary to discuss Professor BARDELEBEN'S views further upon this character of the carpus, because I have obtained new evidence of the structure of the carpus in allied animals (p. 36; Plate 2, fig. 17), with the bones united by matrix, in other genera, demonstrating three bones in the proximal row. And this seems to me confirmatory of the interpretation which I originally offered, since I am aware of no fact tending to a different conclusion.

Professor BARDELEBEN, however, proposed to obtain an additional bone in the central row of the carpus by dividing into two the bone which I have lettered *h* ('Phil. Trans.,' B., 1888, Plate 26, fig. 1), as is shown in his drawing ('Proc. Zool. Soc.,' 1889, plate 30, fig. 4, ce^1, ce^2). For this division I believe there is no justification, either in the specimen, or in the osteology of allied animals, and I have no evidence of it in the example of the carpus which I collected at Lady Frere (Plate 2, fig. 17).

The bone which I have regarded as the innermost central bone, in Professor BARDELEBEN'S nomenclature is the pre-pollex. I have no new evidence on this interpretation, and see no reason to vary my reading; and therefore submit the question to those who examine the original specimen. When I described the fossil, the possibility of there being a digit interior in position to the first occurred to me, but the evidence was too slender to justify me in doing more than (*loc. cit.*, p. 148) record that the first bone of the central "series, counting from the radial side, is situate at the upper inner angle of the trapezium. It is a small ossification, 2 millims. in diameter, and sub-quadrate in form. It may be connected distally with

a minute ossification external to the trapezium." Professor BARDELEBEN does not quote that passage, though he suggests names for the hypothetical bones of the digit thus described. The small bone which is drawn in my figure, external to the trapezium, may be homologous with that named pre-pollex by him in *Bathyergus maritimus*. But it has not been shown that this identification would bring the scapho-lunar bone into contact with the trapezium.

Professor BARDELEBEN has suggested the existence of epiphyses in the phalanges of the third and fourth digits of *Theriodesmus*. During the removal of the bone tissue from the stone I became convinced that the appearance of epiphyses was illusory. It rests entirely upon the shortness of certain phalanges. And the original interpretation was confirmed when I obtained a part of the hand of a larger animal, found near the Oude Kloof, in which the articular surfaces of these short phalanges are well preserved.

On renewed examination of the remains of *Theriodesmus* I fail to find the same preponderance of mammalian affinity in the type as formerly. It is not that there is any change in the value of interpretations of character in the several bones, for the mammalian approximations remain what they were. The whole basis of interpretation has been changed by the discovery of the limb-bones of *Pareiasaurus*. And the revision which I now make shows how closely the reptile *Theriodesmus* may resemble a Mammal, instead of demonstrating reptilian characters in a Mammal as had been inferred.

The humerus of *Theriodesmus* differs in type from every known South African reptile, but is too imperfect to admit of detailed examination of either the proximal or distal end. Its distal end showed a form not unlike that seen in the lion and some marsupials, both in the rounded trochlear reflection of the condyle downward, and in the slight development of the distal crest. These characters make some approximation to those seen in *Pareiasaurus*, which, if not very close, is interesting, since one of the animals compared has slender limbs, and the other has limbs of a remarkably heavy type. The approximation leads me to believe that the imperfect exposure of the proximal end of the humerus of *Theriodesmus* indicates part of a radial crest which I have not seen developed in the same way at the proximal end of the bone in mammals, in relation to its articular head. It also seems evident that the articular head of the bone has not the characteristic curve which is associated in the higher mammals with a more or less hemispherical head. There may be some approach to an ovate form of the head in certain marsupials, but it is only among the Monotremata that this region has a decided horizontal or transverse compression. The difference between the mammalian form of the proximal end, which might be expected from the distal end of the bone in *Theriodesmus*, and the form actually preserved, is shown by shading in a figure already published ('Phil. Trans.,' 1888, vol. 179,

p. 143). The two ends are not in harmony with known mammalia. They seem to me to be better compared with the South African reptilia, because the characters in which the humerus referred to *Cynodraco*, for instance, differs from that of a marsupial Mammal, are most marked in the transverse width of the shallow proximal articulation, and in the proximal development of the radial crest. There being apparently this resemblance to Theriodonts, all of which are distinguished from Mammals by the shape of the articular head of the humerus (in the new examples found by myself), it seems that the humerus of *Theriodesmus* may be regarded as that of a Theriodont, exposed on its external aspect only, and not as that of a Mammal. There is no ground to affirm that the bone is that of a Mammal, because it cannot be paralleled among mammalia. And although the Theriodont limbs are at present imperfectly known, there does not appear to be in the humerus of *Theriodesmus* (fig. 1) any point of structure which may not be paralleled among Theriodonts, and their near allies, and especially in *Pareiasaurus* (fig. 2).

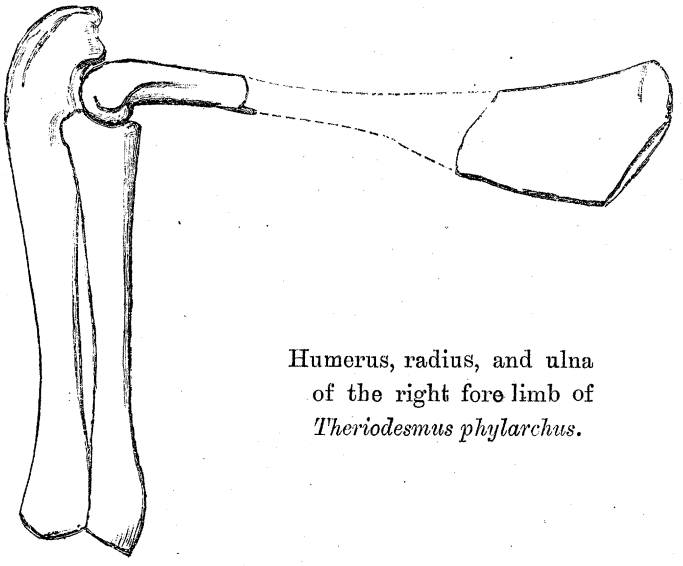
The ulna and radius are much more mammal-like in form, but when those bones were described very little was known of the limb bones of the South African Reptilia. After studying the ulna and radius of *Pareiasaurus* (fig. 2), at Tamboer, it seemed manifest that there is practically no difference of plan between those bones and the corresponding bones of *Theriodesmus* (fig. 1). The difference is essentially one of proportion; part for part and curve for curve they are identical, but the heavy bones of the one are drawn out to a slender type in the other.

The most remarkable character of the ulna in *Theriodesmus* is its prolongation proximally into an olecranon process, which helped to define the articulation for the humerus, and extended beyond it. This process is compressed from side to side; the proximal surface of the bone is concave in length laterally. Its posterior contour is convex as it extends over the olecranon; but the contour becomes concave externally in the lower half of the shaft. These characters are identical in *Pareiasaurus*. In both genera the positions and forms of both proximal and distal articulations are almost identical. In the radius the contours of the bones, which have concave sides and truncated ends, are similar; and in both the articular ends gradually contract to the middle length of the bone, without any approximation to the comparative parallelism of the sides of the bone seen in Mammals, so that the sudden expansion of the articular extremities of the radius, which is commonly found in Mammals, is here wanting. Therefore, notwithstanding the heavier build of *Pareiasaurus*, I have no doubt that *Theriodesmus* makes a nearer approach to that type in the ulna and radius than it does to the corresponding bones of Mammals which approximate nearest to it in form and relative stoutness of the bones.

There are no new facts which illustrate the carpus. *Pareiasaurus* proves to have a proximal carpal beneath the radius, which I have regarded as formed by the scaphoid and lunar bones, as in *Theriodesmus*. I have already indicated ways in which it diverges from Mammals towards some Reptilian types. I have not met with any

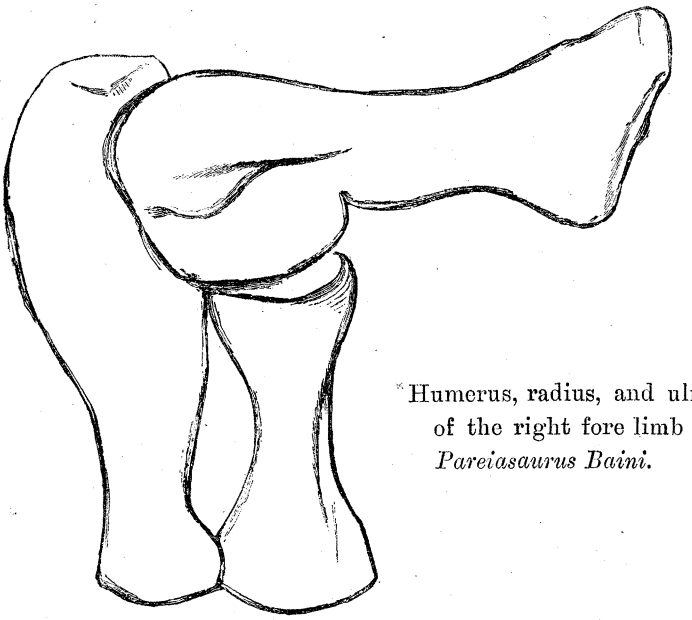
other example of a carpus in which the central bones are similar; but the blending of the scapho-lunar appears to be a character found in the South African Therosuchian reptiles which are known. It is not possible to compare the carpus closely with that of

Fig. 1.



Humerus, radius, and ulna of the right fore limb of *Theriodesmus phylarchus*.

Fig. 2.



Humerus, radius, and ulna of the right fore limb of *Pareiasaurus Baini*.

Pareiasaurus, because the carpus in that type was not extracted in an entire state from the rock. The presence of a second central bone in *Theriodesmus* is a nearer approach to *Hatteria* than to any Mammal; while the possible presence of a third central bone would be a resemblance of an amphibian type.

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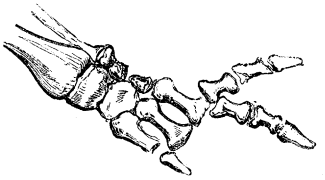
It has already been observed that the metacarpus resembles that of *Protorosaurus* ('Phil. Trans.,' B., 24) and Scaphosaurians, as well as carnivorous Mammals like the Otter and *Thylacynus*.

The evidence no longer appears to me to warrant the view that the extremity of the fourth digit of *Theriodesmus* was lost and replaced by fibro-cartilage. In the impression of the digit preserved, I believe the fourth phalange to be indicated and displaced laterally, so that I mistook it for indications of ligaments. The terminal claw appears to be transverse, beyond the third and fourth phalanges. Hence the number of phalangeal bones in the digits may have been I., 2; II., 3; III., 4; IV., 5; V., 3. If the pre-pollex really exists as a digit, the evidence is not conclusive that it includes more than a metacarpal rudiment. I have no doubt that the hand is more Reptilian than Mammalian, though the phalangeal bones approximate to those of Monotremes in form. *Pareiasaurus* shows no resemblance in having similarly short phalanges between the longer bones. Its digital formula appears to be I., 3; II., 4; III., 4; IV., 3; V., 3.

On this evidence I conclude that *Theriodesmus* is related to *Pareiasaurus* in ways which were unknown when the genus was described. And the resemblances seem to me to be such that there is now ground for placing those types in subdivisions of the same group of animals. It having been proved that *Pareiasaurus* is essentially reptilian in the characters which are of value in classification, it follows that *Theriodesmus* cannot be a mammal. The mammalian resemblances, however, which have been demonstrated in its bones show that the border limit between Reptiles and Mammals approximates so closely in osteological character that the distinction between those groups of animals has not hitherto been easily made on the evidence of the fore-limb. Practically that distinction may be said to have disappeared, for the characters which divide the two groups as now stated are of small value in classification.

Fig. 3.



Carpus of *Herpetochirus*, showing the bones which articulate with the radius and ulna, with part of the metacarpus and phalangeal bones of the digits, in a specimen from Klipfontein.

There is every reason to believe that *Theriodesmus* belongs to that group of animals which approximates to mammalia in its dentition, which Sir R. Owen termed Theriodontia; but as the dentition is unknown there is no means of defining its systematic

position within that group, or of establishing that conclusion, by other than inductive evidence of Pareiasaurian affinities.

II. *On Tritylodon longævus* (Owen). Plate 89, fig. 15.

In 1884, Sir R. Owen described the anterior part of a skull from Thaba-chou, Basutoland, which was associated with remains of *Kistecephalus* and *Batrachosaurus* ('Quart. Journ. Geol. Soc.,' vol. 40, p. 146, plate 6). In its dentition the anterior teeth are placed almost as in rodents; there are no teeth in the usual position of canines; the molar teeth approximate to those of *Stereognathus*, and appear to have the roots divided as among most Mammals. The author concluded that the osteology of the skull showed mammalian conformity with the characters of the teeth.

The evidence which I obtained at Lady Frere of the dentition in new fossil animals which approximate to Theriodont types, leads me to re-examine the osteology of the skull of *Tritylodon*. In its general form the contour of the skull of the reputed Mammal is similar to that seen in reputed Reptiles (Plate 89, figs. 15, 16). This is evident in the mode of development of the parietal crest which bifurcates at its anterior termination in both types, in the way seen in carnivorous Mammalia. The position of the orbit is the same in both types, though in *Tritylodon* only its anterior and inner border is preserved. Sir R. Owen has assumed that the orbit was incomplete on its posterior border, as among carnivorous Mammals, but there seems to me ground for inferring that it was completed posteriorly, as among Theriodonts. The transverse expansion of the sub-orbital and supra-alveolar bar of the maxillary bone (Plate 89, fig. 15 *mx*) is a character common to Theriodonts and Mammals; but its lateral direction is singularly Theriodont (fig. 16 *mx*), for many of the skulls are characterized by a sudden transverse widening at the orbits. This character is associated with a transverse narrowing of the skull in front of the orbits, which gives a somewhat bulbous aspect to the extremity of the snout, due to anterior convexity of the maxillary bones. This character is found in Theriodonts in which, however, it is associated with the extension of the roots of the canine teeth into the maxillary bones, while in *Tritylodon* it results from a similar upward and backward extension of the roots of teeth which have been termed incisors. The circumstance that those teeth do not meet in the median line, but are separated by an interspace wide enough to have contained small incisor teeth, coupled with the fact that indications of successional teeth which have been partly absorbed, but are sometimes not absorbed, are found behind the canines in Theriodonts, makes it doubtful whether those teeth may not be regarded as canines comparable to the canines of Theriodonts, rather than as incisors comparable to the incisor teeth of Mammals like Rodents. The nares are terminal in *Tritylodon* and in Theriodonts. There is a median anterior process of the premaxillary like that which in Theriodonts often forms the inter-narial septum in advance of the alveolar border, and this character

is at least suggestive that the anterior nares may have been conditioned as in Theriodonts rather than as in Mammals, though the small size of the premaxillary bones, and the development of the nasal bones, is similar in both. The posterior nares are conditioned as in Theriodonts, opening between the hinder molar teeth. This character is not mammalian, though Marsupials make an approximation in having the palate more or less largely perforated between the hinder molars. And since the palate is not completely preserved, there is no proof that *Tritylodon* had no posterior transverse bar in the palate such as characterizes Marsupials, though the absence of a bony ledge on the inner border of the hinder molar teeth makes the existence of that marsupial character improbable. As far as the evidence goes the posterior nares are Theriodont.

In view of these resemblances, it may be mentioned that Sir R. Owen thought it possible that the parietal foramen, which is unknown in Mammals, might be indicated at the anterior bifurcation of the parietal crest. This would have placed it in the frontal bone. No foramen exists in the position indicated, and the depression is such as is seen in some Theriodont skulls. If a parietal foramen existed it could only have been situate in the part of the parietal crest which is lost.

The most interesting region of the skull is that which borders the orbit. The fossil shows no obvious post-frontal bone. Therefore, the orbit of the eye appears to differ from that of a Theriodont in not being completed posteriorly by bone. It is just in this position that the skull is fractured. There is no character which better distinguishes the Theriodont skull from that of a Mammal than the presence of a post-frontal bone, which, in all known specimens, forms a transverse bar at the back of the orbit, and it unites with the frontal bone by a squamous suture. It develops posteriorly a plate which extends into the temporal vacuity (Plate 89, fig. 16 *pt.f.*); and, as these plates of the two bones converge backward upon the sides of the frontal bone, they form the front of what has been termed the parietal crest. These characters are shown in skulls of Theriodont genera which I found in South Africa.

Tritylodon has no trace of the transverse bar of the post-frontal bone behind the orbit, but the fossil shows an oblique fracture on the left side at the back of the orbit, and on the right side there is an indication of a transverse fracture with the matrix still in contact with the broken bone. This fracture is shown in Sir R. Owen's figure ('Quart. Jour. Geol. Soc.,' vol. 40, Plate 6, fig. 1) behind the letter *v*. Behind these fractures, the bones converge backward between the temporal vacuities, to form the median crest. Those converging plates were described by Sir R. Owen as the parietal bones. Their posterior fracture shows a vertical median suture, but the lateral sutures are not manifest which might be expected to separate them from the frontal bones, and it is possible that they rise to a superior position and unite above the frontal bones. I have no doubt that they are the posterior processes of the post-frontal bones, because they are closely comparable with the similarly placed bones of Theriodonts, and that the structure of this part of the skull is not paralleled in Marsupials, or other Mammals, which have the parieto-frontal suture placed further

backward than in Sir R. Owen's figure. The broken lateral surfaces which I have described indicate a structure now lost which apparently extended outward from the back of the orbit. It is, therefore, in the position of the transverse bar of the post-frontal bone, but appears to have been more slender than in any Theriodont known at present, which approximates to *Tritylodon* in form. Thus, although the post-orbital bar is unknown, the evidence seems to me to warrant the conclusion as highly probable that it was present in the complete skull and defined the back of the orbit as in Theriodonts.

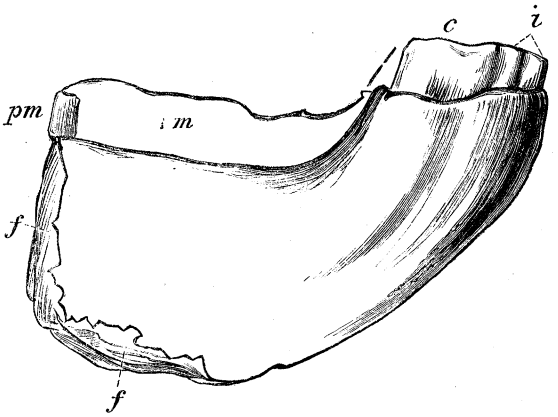
The pre-frontal bone is distinctly shown in Sir R. Owen's figure 1, forming the antero-superior border of the orbit. Its posterior border is impressed by the missing part of what I have regarded as the post-frontal bone, so that the pre-frontal and post-frontal bones united above the orbit, and excluded the frontal from the orbital border, as among Theriodonts. The presence of a pre-frontal bone is a reptilian character unknown among Mammals, and its identification has some bearing on the value of the recognition of the post-frontal. The pre-frontal bone (Plate 89, fig. 15 *pr.f*) has an external superior surface above the front of the orbit, which is $\frac{13}{20}$ inch long, being a long triangle $\frac{7}{20}$ inch wide in front where widest. It is margined externally by a sharp angular ridge, which separates the superior area from the internal orbital area, which is nearly vertical, flattened, a little concave, looks outward and backward, and appears to be $\frac{9}{20}$ inch deep. Anteriorly the bone joins the lachrymal bone by a well-marked suture.

The lachrymal bone shows the usual external area in front of the orbit, which is $\frac{9}{20}$ of an inch long and $\frac{12}{20}$ inch deep. It meets the maxillary bone below and in front, and joins the frontal and pre-frontal above. The frontal bone is $\frac{19}{20}$ inch wide at the widest point, where the lachrymal joins the pre-frontal. A sharp marginal ridge, continuing that of the pre-frontal, separates the external surface from the internal posterior orbital surface of the lachrymal bone, on which the lachrymal foramen is seen.

The identification of the pre-frontal and post-frontal bones is in harmony with the other resemblances to Theriodonts, which have been enumerated. Hence I believe that what remains of the skull goes to show that *Tritylodon* was a Reptile, and that the skull might be restored upon the Theriodont plan. If the teeth had been unknown it would have been difficult to find grounds upon which it could have been referred to the Mammalia, since the only character in which it differs from Theriodonts is the vertical elevation and median union of what I have regarded as posterior plates of the post-frontal bones. The other parts of the skull at present unknown may have been as reptilian as those of Theriodonts. It follows that if *Tritylodon* is classed as a Reptile on the evidence of skull structure now stated, it has molar teeth, with complicated cuspidate crowns, and long, straight, divided roots apparently, such as are only known in Mammals. It is the only animal at present known in which these characters are combined with reptilian skull structure. So far the genus

may be said to be more Mammalian than any known Theriodont. But just as the development of divided roots to molar teeth is not a general character among Mammals, so the presence of double roots to the molars of *Tritylodon*, if established, may only show that the character is found in Reptiles which approximate to Mammals in many other characters. Some of the lower Mammalia have two roots to the canines, as is well known; and others appear to have two roots to the incisors. *Perameles nasuta* (R. Coll. Surg., 3876) has a double-rooted incisor seen in the translucent premaxillary bone in advance of the functional canine, which has a single root. In *Petrodromus tetradactylus* the last tooth in the premaxillary appears to have the root divided (R. Coll. Surg., 3368). There is no evidence of this kind of variation in the roots of teeth among Reptiles, recent or fossil, so that the character may be important enough to place *Tritylodon* in a group of animals intermediate between Mammals and Theriodonts. One feature in the arrangement of the molar teeth is an obvious resemblance to Mammals, for those of the two sides of the jaw are straight and nearly parallel; while in Theriodonts they are frequently, though not invariably, curved, and diverge as they extend backward.

Fig. 4.



Anterior extremity of the right ramus of a mandible.

Other animals may become known hereafter which are allied to *Tritylodon*. In 1889 I examined in the South African Museum at Cape Town a small fragment of the right ramus of the lower jaw, obtained by Dr. KANNEMEYER from near Burghersdorp in 1884. It is fractured (*f*) behind the first pre-molar tooth. It shows three (or possibly four) small, cylindrical, close-set incisor teeth (*i*), with the crowns broken. The canine (*c*) is in close contact with the incisors. It is ovate, with flattened sides, and has its long axis in the length of the jaw. It measures half-an-inch from front to back. Behind the canine there appears to be a toothless diastema (*m*) occupied with matrix, which is concave in length, and more than one and a half-inch long between the canine and the small first pre-molar (*pm*), which appears to be subquadrate. The animal was larger than *Tritylodon*, and has incisors and canines of the usual type. The general form of the jaw is such as might be expected in *Tritylodon*.